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Data Paper

Annotated inventory of invasive social wasps (Hymenoptera, Vespidae) in the South Pacific, excluding Australia and Papua New Guinea

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Abstract

This paper presents an annotated inventory of the alien social wasps (Hymenoptera: Vespidae: Polistinae, Vespinae) of the South Pacific Oceanic islands, excluding Australia and Papua New Guinea. Here we include information on invasive social wasp distribution, known introductions and establishment dates, and notes on their invasive ecology. Introduced social wasps in the South Pacific consist of 11 species belonging to the Polistinae (*Polistes*: n = 7) and Vespinae (*Dolichovespula*: n = 1; *Vespa*: n = 1; *Vespula*: n = 2), nine of which are known to have established across the Pacific. Introduced species were recorded in nine countries and territories (Cook Islands, Easter Island, French Polynesia, Fiji, New Caledonia, New Zealand, Niue, Samoa, and Tonga), with the earliest records having happened between the 19th century and the present day. We also provide novel commentary on the ongoing and recently detected incursion of *Vespa velutina* (an established and impactful invasive species in Europe) into New Zealand. This inventory provides a resource to further understand the invasion biology of social insects and to scaffold risk modelling and management efforts for a taxon of impactful invasive predators in a severely understudied area.

Key words: Aculeata, Biological invasions, Invasive insects, Pest management, Paper wasps

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Introduction

The eusocial Hymenoptera (infraorder Aculeata; social bees, social wasps, and ants) are some of the most impactful invaders of terrestrial ecosystems. Their unique reproductive biology facilitates the incursion of undetected gynes into new areas, often escaping "wide net" approaches to biosecurity practices (Ayer and Vargo 2021). Following an incursion, their complex social organisation – including task specialisation afforded by division of labour – often operates in tandem with highly adaptable foraging behaviours (Manfredini et al. 2019), allowing insect colonies to quickly establish in and dominate novel environments. Invasive social insects impact native arthropod fauna through predation, competition for resources, and pathogen spread (Bertelsmeier 2021), operating change at the landscape level. Furthermore, the nest defence behaviours of the stinging aculeates also presents a significant issue for human health and wellbeing (Costa et al. 2018; Feás 2021). Some of the most notable ongoing terrestrial biological invasions feature social insects (e.g. Argentine and red imported fire ants worldwide: Allen et al. 2004; Silverman and Brightwell

2008; yellow-legged Asian hornets in Europe: Barbet-Massin et al. 2020). Billions of dollars are spent annually worldwide by governing bodies and the private industry to manage socioeconomical and ecological effects of these alien communities (Lester and Beggs 2019; Barbet-Massin et al. 2020; Angulo et al. 2022).

The Oceanic Islands of the South Pacific are an area of interest when considering social insect invasions. Mostly comprised of spaced, geologically young islands (Neall and Trewick 2008), the region shows a remarkably low native diversity for some taxa of social aculeates. This is especially true for social wasps (Hymenoptera: Vespidae: Polistinae, Vespinae). Despite geographic proximity to the taxa's biodiversity hotspot in Southeast Asia and Australasia (Carpenter and Brown 2022), most of the South Pacific has few to no known native social wasps. The absence of eligible natural enemies and competitors may be one of the factors driving the region's well studied cases of successful and impactful social wasp invasions. The *Vespula* introductions in New Zealand have caused catastrophic ecological imbalance and decimate endemic arthropod and vertebrate fauna, which they prey upon and/or displace through out-competition (Lester and Beggs 2019). Some of the most widespread social wasp invaders worldwide (e.g. *Polistes olivaceus*: Beggs et al. 2011) have also been recorded throughout multiple islands. Social wasp incursions in the South Pacific are ongoing, with the most recent known example being the recently detected populations of *Vespa velutina* in New Zealand as late as October 2025 (Ministry of Primary Industries 2025). As conservation and biosecurity priorities are established for safeguarding Pacific native biodiversity (Dovey et al. 2004; Hoffmann et al. 2024), special attention must be given to these high-profile, successful invaders.

Despite wide acknowledgement of the severity of social wasp invasions in the South Pacific (Beggs et al. 2011; Cook 2019; Lester and Beggs 2019; Wilson Rankin 2021), data on these taxa for the southern Oceanic Islands is scattered across the scientific literature, often focused on narrower taxonomic groupings and on individual countries. This makes the understanding of invasion history and ecology difficult and hinders efforts to accurately model invasion risk. Aiming to bridge this gap, our objective was to create a current and accessible annotated inventory of invasive social wasp species for the South Pacific. We build on previous research papers and comprehensive checklists, notably Carpenter (1996) and Carpenter and Brown (2022), to provide a centralized dataset for the South Pacific islands which can be used as scaffolding for future trans-Pacific biosecurity and conservation efforts, as well as invasion ecology investigations for the social Vespidae. Here, we provide an annotated list of the invasive species from subfamilies Vespinae and Polistinae in the region, including a summary of their known invasion history and findings on their ecology in their Pacific invaded ranges. We also provide novel commentary on the current *Vespa velutina* incursion into New Zealand, including ongoing eradication efforts following its detection in 2025.

Methods

Area and scope of study

For the purpose of this inventory, we define "South Pacific" as the area including the cultural areas of Melanesia and Polynesia south of the Equator, limited by Australia and Papua New Guinea to the west and Easter Island to the east. It is important to note that both Australia and the island of Papua New Guinea were not included

in our datasets. This was done due to both areas presenting starkly different social vespid community structures when compared to other South Pacific territories. The two excluded regions have diverse native social wasp faunas, which are both somewhat well studied and contiguous with Southeast Asia (Carpenter 1996; Carpenter and Brown 2022). Other South Pacific islands, in contrast, are almost all devoid of extant, native social wasps (with a few exceptions on the westernmost areas) and often have their social wasp communities dominated by one or a few alien species. Therefore, and despite the presence of noteworthy and invasive social vespids (e.g. *Vespula* in Australia: Spradbery and Maywald 1992; Matthews et al. 2000), we decided not to include them in this inventory to allow for a consistent discussion on areas suffering from similar pressures from an invasion ecology perspective.

To build the inventory, we listed species of social wasps (Hymenoptera: Vespidae: Polistinae, Vespinae) known to have been introduced in recent human history. We avoided ambiguity in invasive status wherever possible. All species included in this list are known to be native outside the South Pacific and have first record/invasion occurrences documented with some clarity. Species that are native to the South Pacific (e.g. *Polistes stigma nebulosus* Yamane & Kusigemati, 1985 in Fiji and the Solomon Islands; Yamane and Kusigemati 1985) were not included in the inventory. Similarly, species which may have originated outside the area of study, but whose native range has come to include the South Pacific before modern faunal records (either through ancient, man-facilitated or self-introductions) were also not included in our dataset. Examples of these occurrences include *Polistes tepidus malayanus* Cameron, 1906 in Vanuatu (Carpenter 1996) and *Ropalidia impetuosa* (Smith, 1861) in Fiji and the Solomon Islands (under synonym *Ropalidia gregaria* Sausurre, Yamane and Kusigemati 1985). On the other hand, we chose to include failed (non-established) known incursions of alien social vespids in our dataset (e.g. *Dolichovespula maculata* and *Polistes olivaceus* in New Zealand: Harris 1984; Thomson 1923), as this information provides relevant insights to the discussion on the biosecurity and invasion ecology of social wasps in the South Pacific. Only taxa identified down to species level were included in this inventory.

Literature search and data curation

In order to produce a robust and up-to-date inventory of social Vespidae in the South Pacific, we modified the workflow suggested by Simpson and Eyler (2018) (based on Kissling et al. 2017) for creating Essential Biodiversity Variable datasets. Social wasp introductions in the South Pacific were scoped from the scientific literature using an exploratory review approach. We searched the Web of Science and Google Scholar repositories using taxonomy-related keywords ("Vespidae", "Polistinae", "Vespinae", "social wasp*") coupled with both general geographical keywords (e.g. "Pacific", "Oceania") and specific ones relating to each country, territory, or region within our area of study (e.g. "Fiji", "New Zealand", "Tuoamotu Archipelago"). Results from this search were used to generate an exploratory dataset with candidate taxa and areas for social wasp introductions in the South Pacific. Based on these data, a second, comprehensive search was carried out at the same repositories with specific search queries (e.g., "*Polistes aurifer*" + "French Polynesia") to obtain precise data referring to first records of introductions and invasive range for each recorded taxon and area. This second search was used to generate our final dataset.

To check for data quality and clean the final dataset, we referred to the GBIF (2025) database, as well as comprehensive and authoritative social Vespidae

checklists published by Carpenter (1996) and Carpenter and Brown (2022). This step allowed us to check for deprecated taxonomic synonyms, as well as identify original introduction records and other records not present in scientific literature (e.g., entomological collection entries).

Results

Our literature search revealed 11 alien species of social wasps to have been reported across the South Pacific, two of which being represented by distinct subspecies (*Polistes stigma bernardii* and *P. stigma townsvillensis*, *P. humilis humilis* and *P. humilis synoecus*). These invasive taxa belong to four genera across the subfamilies Polistinae (*Polistes*, n=7) and Vespinae (*Dolichovespula*, n = 1; Vespa = 1; and *Vespula*, n = 2). Nine out of the 11 species have successfully established in at least one place in the studied area (with the exception of *Dolichovespula maculata*, which failed to establish in New Zealand, and *Vespa velutina*, which is a recent and ongoing incursion in the same area) across a total of nine countries/territories. Introductions are indicated to have happened mostly in the 20th century, especially in earlier decades; a single introduction dates from the 19th century, and few later ones have been recorded in the 2000s, 2010s, and 2025 (*V. velutina* in New Zealand). Fig. 1 shows a map of the study area showing the distribution of social wasp invaders and their earliest record dates.

Below, we include an annotated inventory of each recorded invasive species of social wasp in the South Pacific. The entries are organized alphabetically by subfamily, genus, and species, in that order. For each entry, we provide a summary of their native distribution range, known invasive range in the South Pacific, and notes from studies on its invasive ecology. Visual data on the species' morphology and current distribution are presented in Fig. 2 (Polistinae) and Fig. 3 (Vespinae). Details on earliest records for each taxon and area, as well as materials examined and other evidence, are available in the supplements (Suppl. material 1).

Subfamily Polistinae Lepeletier, 1836
Genus *Polistes* Latreille, 1802

Polistes aurifer de Saussure, 1853

Native range. North America: Northwestern Mexico, Western U.S.A. and Canada (MacLean et al. 1978; Carpenter 1996).

Invasive range. French Polynesia: Society Islands (Bora Bora, Huahine, Raiatea, Tahiti) (Cheesman 1928; Johnson 2020). Also introduced in Hawai'i, U.S.A., in the 19th century (Blackburn and Kirby 1880; Kirby 1884).

Notes on invasion ecology. The earliest record is from 1925 by Cheesman (1928), with few male and several female specimens found in Bora Bora, Raiatea, and Tahiti, Society Islands. No further information on site, nests, or general invasion were provided. First hand records of *P. aurifer* in French Polynesia are remarkably scarce, although specimens collected as late as 2012 (Johnson 2020) suggest that the species has established in the area since its first record. There are no published data on the invasive ecology or impacts of *P. aurifer* in French Polynesia. Similarly, studies on *P. aurifer* in Hawai'i are also lacking, although the species has been observed to be a vector of Deformed Wing Virus, an impactful disease for the apicultural sector (Santamaria et al. 2018).

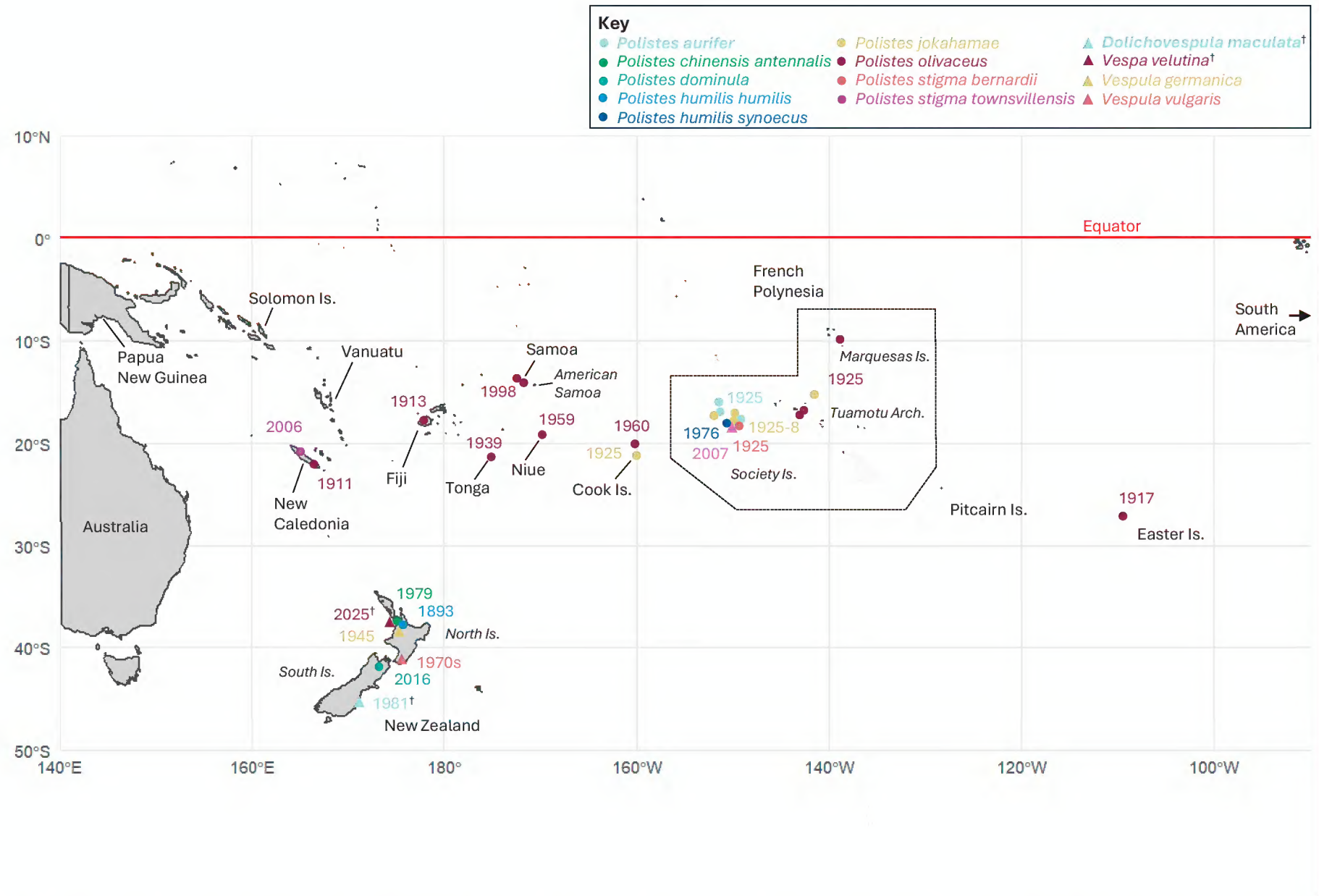

Figure 1. Map of social wasp invasions (Hymenoptera: Vespidae: Polistinae, Vespinae) in the South Pacific islands, excluding Australia and Papua New Guinea. Dots and triangles on the map are coloured to represent each of the different taxa, including dates for the single earliest record in each country or territory; dots are used to indicate taxa belonging to the Polistinae subfamily, while triangles are used to indicate taxa belonging to Vespinae. Position of dots and triangles and scale on the map are approximated for representation, and do not accurately georeference record sites. Taxa marked in the key and map with a cross (†) represent incursions that were not or are not yet confirmed to have led to establishment. The area within dashed lines represents the approximate territory of French Polynesia, encompassing multiple archipelagos. Map was created in R v.3.4.2.1 (R Core Team 2025) using the package 'maps' (Becker et al. 2024).

Polistes chinensis Fabricius, 1793
Subspecies *P. chinensis antennalis* Perez, 1905

Native range. Central to Eastern Asia: China (incl. Hong Kong, Taiwan); Japan; Korea; Russia (Siberia) (Carpenter 1996; Tsuchida et al. 2014; Carpenter and Brown 2022).

Invasive range. New Zealand: North Island; northern to central South Island along east coast; recorded in offshore islands (Clapperton et al. 1996; Tsuchida et al. 2014). Also introduced in Australia, established by 2008 (Beggs et al. 2011).

Notes on invasion ecology. First recorded in New Zealand's North Island in 1979, having been repeatedly sampled in the decade following its discovery (Clapperton et al. 1989b). Until the 1990s, it remained restricted to northern and central North Island, having spread to the South Island and offshore islands since then (Clapperton et al. 1996; Tsuchida et al. 2014). There is no information available on invasion pathways of *P. chinensis* into New Zealand, although molecular evidence suggests at least two independent introductions from distinct Japanese populations (Tsuchida et al. 2014). Populations of *P. chinensis antennalis* have been reported in a range of environments but seem to favour urban ones (Clapperton et al. 1996; McGruddy et al. 2021) and have been estimated to significantly impact native invertebrate populations which can comprise up to 50% of its diet (Howse et al. 2022; Reason et al. 2024).

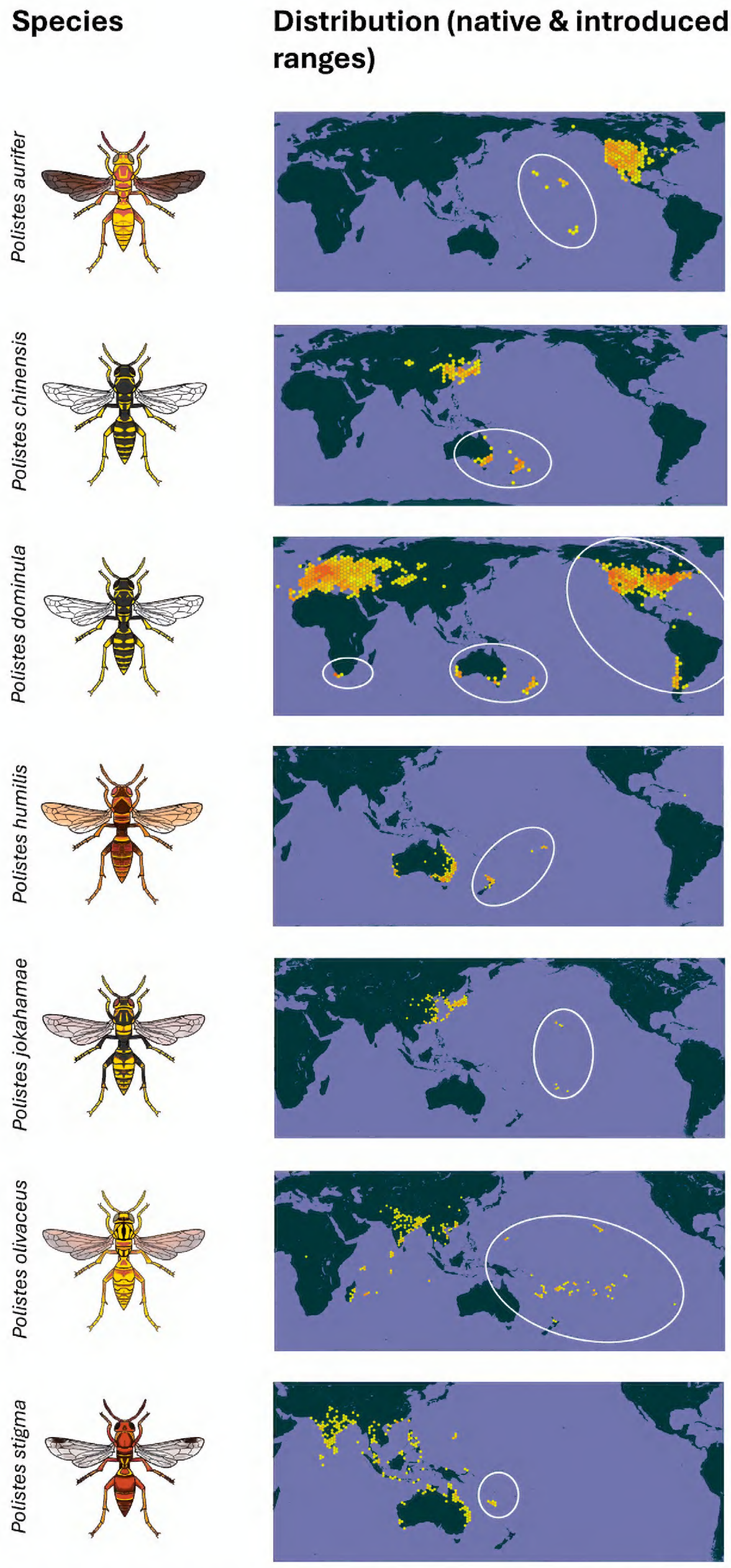

Figure 2. Alien social Polistinae found in the South Pacific and their global distributions. Species column illustrations are of adult females. Maps in the Distribution column represent known geographical distribution for each wasp species (https://www.gbif.org/; references for individual species occurrence data in Suppl. material 2). Warmer coloured areas have higher numbers of observations and where the species are introduced or invasive are outlined with white lines. *Polistes olivaceus* has been detected in New Zealand many times but is not known to have established.

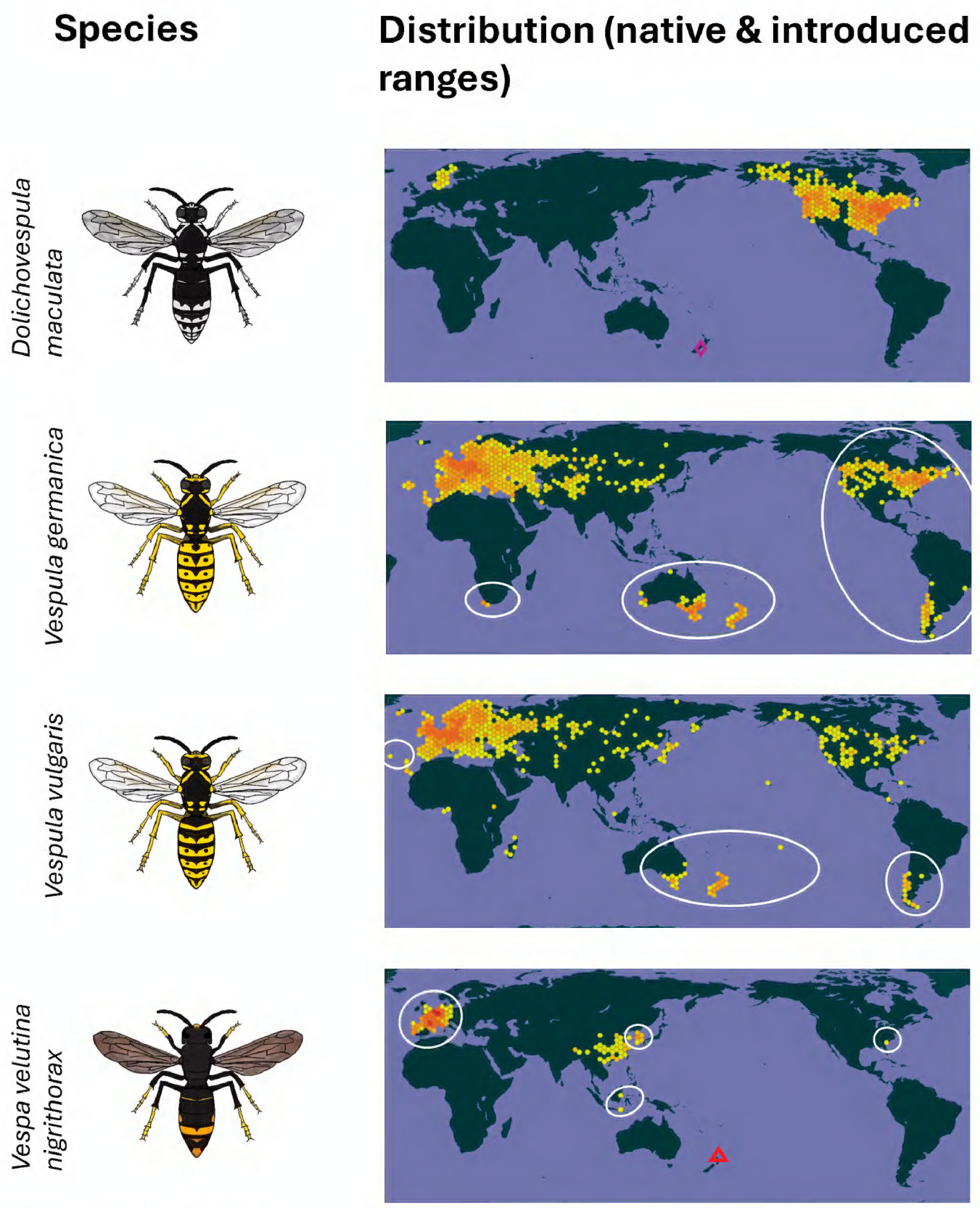

Figure 3. Alien social Vespinae found in the South Pacific and their global distributions. Species column illustrations are of adult females. Maps in the Distribution column represent known geographical distribution for each wasp species (https://www.gbif.org/; references for individual species occurrence data in Suppl. material 2). Warmer coloured areas have higher numbers of observations and where the species are introduced or invasive are outlined with white lines. Recent detections of *Vespa velutina nigrithorax* in New Zealand are represented by a red triangle, currently not known to be established. *Dolichovespula maculata*, represented with a purple diamond, were detected in New Zealand in the early 1980's but never established.

Polistes dominula (Christ, 1791)

Native range. Europe: originates in the Mediterranean (Carpenter 1996; Guiglia 1972), expanded to include most of Southern and Central Europe, potentially still expanding northwards (Kovac et al. 2017); Northern Africa; Asia: China, Middle East, and Russia (Cervo et al. 2000).

Invasive range. New Zealand: North Island (especially Auckland), northern to central South Island along east coast (Howse et al. 2020). Highly invasive worldwide: also established in Australia by 1977 (Cardale 1985); introduced in areas of Africa (Eardley et al. 2009; Gereys et al. 2019); North America (Cervo et al. 2000; Borkent and Cannings 2004); South America (González 1989; Sackmann et al., 2003); St. Helena Island (Gray et al. 2019).

Notes on invasion ecology. First recorded in New Zealand's South Island across a few sites in 2016, assumed to be already having been present years prior (Ministry of Primary Industries 2016). *P. dominula* seems to remain most abundant in the northern South Island but has spread southwards considerably and is also recorded in the North Island, especially around Auckland (Howse et al. 2020). There is no available information on invasion pathways or phylogeography of *P. dominula* populations in New Zealand. Molecular investigations of its diet have shown similar patterns to its co-invader *P. chinensis antennalis*, albeit with an estimated higher proportion of native invertebrates preyed on by *P. dominula* (well over 50%; Howse et al. 2022).

Polistes humilis **Fabricius, 1781**
Subspecies *P. humilis humilis* (Fabricius, 1781)

Native range. Oceania: eastern and southern Australia (Richards 1978; Carpenter and Brown 2022).

Invasive range. New Zealand: North Island (especially Auckland and Northland) (Thomson 1922; Richards 1978).

Notes on invasion ecology. First social wasp reported to establish in New Zealand, recorded from 1893 (Thomson 1922) under the synonym "*Polistes tasmaniensis*". Thomson (1922) reported that it "was extremely common in the north" (of the North Island), where it impacted populations of the invasive cherry and peach slugworm (*Caliroa cerasi*). Miller (1919) also reported the wasps' presence under the synonym "*Polistes tasmanicus*". Although present in northern New Zealand for over 100 years, *P. humilis* have not yet successfully established in the South Island (Clapperton et al. 1996). Clapperton et al. (1996) suggest that *P. humilis* is likely being outcompeted by the invasive *P. chinensis.* Diet studies in New Zealand show that these wasps feed on invertebrates (mostly Lepidopteran larvae), both native as well as agricultural pests such as *Pieris rapae* (Clapperton 1999; LeFort et al. 2020).

Subspecies *P. humilis synoecus* de Saussure, 1853

Native range. Oceania: eastern Australia (Richards 1978; Carpenter and Brown 2022).

Invasive range. French Polynesia: Society Islands (Moorea, Tahiti) (Richards 1978; Gusenleitner 2011). Also introduced in western Australia (Carpenter 1996; Carpenter and Brown 2022).

Notes on invasion ecology. The earliest records of *P. humilis synoecus* in the Society Islands are probably an unspecified number of specimens collected from Tahiti and Moorea, likely in the early 20th century (Richards 1978). Eight females and one male were collected in Tahiti in 1976 (Gusenleitner 2011), suggesting establishment (Carpenter and Brown 2022). No other information on its invasive biology or impact has been published to date.

Polistes jokahamae **Radoszkowski, 1887**

Native range. Asia: China (including Taiwan), India, Japan (including Ryukyu Islands), and Korea (Starr 1992; Carpenter 1996; Choi et al. 2013).

Invasive range. Cook Islands: Southern Islands (including Aitutaki, Atiu, Mangaia, Mitiaro, Mauke, and Rarotonga) (Bernice Pauahi Bishop Museum 1997; Kuhlmann 2006; Landcare Research 2025); French Polynesia: Society Islands (Moorea, Bora Bora, Tahiti), Tuamotu Archipelago (Napuka) (under synonym "*Polistes macaensis tahitiensis*": Cheesman 1928; under synonym "*Polistes jadwigae*": Carpenter 1996; Landcare Research 2025); potentially introduced to the Pitcairn Islands (Benton 1995). Also introduced in Hawai'i, present in Oahu by 1905 (Matsunaga et al. 2019).

Notes on invasion ecology. The first record in the Cook Islands (Rarotonga) dates from 1925, with subsequent records in the 1960s, 1970s, and 2000s (Kuhlmann 2006). First record in French Polynesia also dates from 1925, with a single male sampled from the Tuamotu Archipelago (Napuka) and several males and females collected in the Society Islands (Bora Bora, Tahiti) (Cheesman 1928). Several adults were later collected in the Society Islands (Moorea) in 1928 (Landcare Research 2025). Formal records of *P. jokahamae* in French Polynesia become scarce following its initial discovery. Also potentially introduced to the Pitcairn Islands; an unidentified *Polistes* species has been recorded to be abundant in the area (Benton 1995) and *P. jokahamae* has figured in local postal stamps (Stanley Lisica 2025), though there is not enough scientific evidence to support this claim. There are no known studies on invasive ecology of *P. jokahamae* in the South Pacific other than Kuhlmann (2006), who observed the species to be widespread in "open habitats" on the Cook Islands, but less abundant than co-invader *P. olivaceus* populations.

Polistes olivaceus DeGeer, 1773

Native range. Africa: Amirante Islands, Egypt, Madagascar, Mauritius, Réunion, Seychelles, and Tanzania; Asia: Afghanistan, Cambodia, Chagos Archipelago, China (southern), India, Indonesia, Iran, Japan (Okinawa), Laos, Myanmar, Nepal, Oman, Philippines, Singapore; Sri Lanka, Taiwan, Thailand, and Vietnam (Carpenter 1996; Carpenter and Brown 2022).

Invasive range. Cook Islands: Aitutatki (additionally under synonym "*Polistes macaensis*": Krauss 1961); Easter Island (under synonym "*Polistes hebraeus*": Wynne et al. 2025); Fiji: Viti Levu, Tailevu, and Ovalau (Williams 1947); French Polynesia: Tuamotu Archipelago (Fakarava), Marquesas Island (Hiva-oa, Tahuata) (under synonym "*Polistes macaensis*": Cheesman 1928); New Caledonia: southern New Caledonia (notably Noumea) (under synonym "*Polistes hebraeus*": von Schulthess 1915; Williams 1945); New Zealand (not established, under synonym "*Polistes* hebraeus": Thomson 1923; Harris 1979); Niue (under synonym "*Polistes* hebraeus": Given 1968); Samoa (under syns. "*P*olistes *hebraeus*" and *"Polistes macaensis*": Kami and Miller 1998); Tonga (Harris 1979). Also invasive in Oceania: Marianas Islands (Bequaert and Yasumatsu 1939), and Hawai'i (Perkins 1913; Williams 1926).

Notes on invasion biology. There is some uncertainty in the literature as to the native versus invasive range of *P. olivaceus.* Considering that it is the most widespread introduced social wasp in the Pacific, very little is known about its invasion ecology (Beggs et al 2011). Veitch's 1917 report titled "The Hornet in Fiji" (under synonym "*Polistes hebraeus*"), thoroughly describes the biology and impacts of the invasive wasps in Fiji with regard to the operation of sugar cane production. Veitch (1917) mentions that the exact date of *P. olivaceus* arrival to Fiji is unknown, but that it was detected in Suva by 1904 and speculated that it likely arrived on a ship

from either India or Hawai'i. While stating that the wasps are "a distinctly useful addition to our fauna" as they are important for regulating insect pests of the cane crops, he also says the wasps are "the cause of considerable annoyance to the plantation labourers, who are frequently severely stung" (Veitch 1917). In New Zealand, two specimens of *P. olivaceus* (likely workers) were found in 1921 in Auckland, North Island, one of which was hypothesized to have "escaped from a consignment of island fruit" (Thomson, 1923), but the species failed to establish in the country.

Polistes stigma Fabricius, 1793
Subspecies *P. stigma bernardii* Le Guillou, 1841

Native range. Oceania: Australia (across northern areas and Queensland); New Guinea (Richards 1978; Carpenter and Brown 2022).

Invasive range. French Polynesia: Society Islands (Tahiti) (under synonym "*Polistes bernardi*", Cheesman 1928).

Notes on invasion ecology. First and only record in the literature is from the Society Islands (Tahiti) in 1925, with the sampling of five males, one worker, and one queen (Cheesman 1928). There are no formal recent records of *P. stigma bernardii* in Tahiti or elsewhere in French Polynesia, with the latest references (Carpenter 1996; Carpenter and Brown 2022) being based on its original one. No studies on its invasive biology or impact have been published to date.

Subspecies *P. stigma townsvillensis* Giordani Soika,1975

Native range. Oceania: widely distributed in Australia (Carpenter and Brown 2022).

Invasive range. New Caledonia (Jourdan and Mille 2006).

Notes on invasion ecology. Observed in New Caledonia as early as 2006 (Jourdan and Mille 2006), and since then included in the Global Register of Introduced and Invasive Species for New Caledonia (Barrière et al. 2020). No studies on its invasive biology or impact have been published to date.

Subfamily Vespinae Latreille, 1802
Genus *Dolichovespula* Rohwer, 1916

Dolichovespula maculata (Linnaeus, 1763)

Native range. North America: widespread in most of Canada and the U.S.A. (Carpenter and Kojima 1997; Akre et al. 1980).

Invasive range. Absent in the South Pacific (see notes). Potentially invasive in Northern Europe (Sweden and Denmark), based on recent genetic marker sampling efforts (Miraldo et al. 2025).

Notes on invasion ecology. Live queens were captured in urban South Island sites in New Zealand (Dunedin and Christchurch) between 1981 and 1982 (Harris 1984). It has been speculated that they might have been accidentally imported through cargo ships into both city's ports. The species failed to establish in the country and is not known to be an invader elsewhere in the Pacific. Its failure to establish is potentially due to the capturing of queens before nest foundation (Harris 1984).

Genus *Vespa* Linnaeus, 1758

Vespa velutina Lepeletier, 1836

Native range. Asia: Afghanistan; Bhutan; China (southern, including Hong Kong and Taiwan); India; Indonesia; Laos; Malaysia; Myanmar; Nepal; Pakistan; Thailand; Vietnam (Smith-Pardo et al. 2020).

Invasive range. Asia: Korea; Japan; Yemen (Smith-Pardo et al. 2020). Europe: confirmed subspecies *V. velutina nigrithorax* (de Buysson, 1903) in Belgium, France; Italy, Portugal, Spain, and United Kingdom (Monceau et al. 2014; Smith-Pardo et al. 2020; Lioy et al. 2023). Oceania: recently recorded as a new arrival in New Zealand, likely *V. velutina nigrithorax* (North Island: Auckland; Ministry of Primary Industries 2025).

Notes on invasion ecology. *V. velutina nigrithorax* has been thoroughly documented in its recent invasion of Western Europe. The introduction event is hypothesised to have occurred through a single incursion by accidental sea transport inside imported pottery from China to France around the early 2000s (Rortais et al. 2010; Arca 2012; Monceau et al. 2014), from which it has steadily spread to neighbouring countries. *V. velutina* life cycles, population ecology, nesting behaviour, diet, ecological and economic impacts, and accidents with humans have been the subject of various studies over the last decade (Villemant et al. 2011; Arca 2012; Monceau et al. 2013a; Monceau et al. 2013b; Feás 2021; Lioy et al. 2023). In Europe, a suggested key factor contributing to its establishment success has been a partial specialisation in foraging on commercial beehives (*Apis mellifera* L.), which can make up over 30% of a colony's diet (Villemant et al. 2011). Unlike the honeybee species which coevolved with *V. velutina* in their native range (notably *Apis cerana* Fabricius, 1793; Ken et al. 2005), *A. mellifera* colonies typically lack effective anti-predator defences to deter a *V. velutina* raid. The exploitation of honeybees as a domesticated, widespread prey species likely plays a role in enabling *V. velutina*'s potential as worldwide invader.

Recently, in the Austral spring of 2025, multiple colonies of *V. velutina* (likely *V. velutina nigrithorax*) were discovered in the North Island of New Zealand. As of December 2025, more than 17 nests and 30 queens have been located and destroyed (Ministry of Primary Industries 2025). The invasion pathway for *V. velutina* in New Zealand has not yet been elucidated, though the entry point being geographically close to the country's busiest port region points toward accidental transport in commercial vessels (as generally hypothesised for other social wasp invaders in the area). These early findings suggest that the introduction also happened in the 2024–2025 warm season; the dense, clustered population is likely to be the first generation of post-hibernation offspring following an undetected introduction. Currently, New Zealand's Ministry of Primary Industries is conducting an eradication campaign with the help of European experts (Ministry of Primary Industries 2025), in an attempt to prevent the establishment of *V. velutina* in the country. New Zealand's temperate climate and introduced biodiversity presents a comparable setting to *V. velutina*'s Western European invaded range (Hulme 2020), including a strong apicultural industry across islands which could provide invading *Vespa* with a plentiful prey supply. These similarities suggest that establishment is likely if the invasion is not readily contained, which raises public concerns for ecological, economical, and social consequences in New Zealand. Early invasion stages

are critical for the establishment of alien species (or the prevention thereof, Reaser et al. 2020); should ongoing eradication efforts fail, *V. velutina* will become the first of its genus to be recorded as a successful invader in the South Pacific.

Genus *Vespula* Thomson, 1869

Vespula germanica (Fabricius, 1793)

Native range. Widely found across Europe, Northern Africa, and most of Asia (Edwards 1984; Carpenter and Kojima 1997; Archer 1998).

Invasive range. New Zealand: widespread (Clapperton et al. 1994); also introduced in Australia, originally in Tasmania, later across mainland (Crosland 1990; Carpenter and Brown 2022). Also introduced in Africa: South Africa (Whitehead and Prins 1975); Ascension Island (Yarrow 1967); Europe: Iceland (Ólafsson 1991); North America: Canada and USA (Akre et al. 1980; Archer 1998; Buck et al. 2008); and South America: Argentina and Chile (Peña et al. 1976; Willink 1980; D'Adamo et al. 2002).

Notes on invasion ecology. Observed in New Zealand as early as 1922, but not established until 1945; first introduction is attributed to accidental transport of hibernating queens in military aircraft (Thomas 1960). It was widespread in the North Island by 1951, and throughout the country by the 1990s, though somewhat limited to lower altitudes, and displaced in some habitats by the later co-invader *V. vulgaris* (Clapperton et al. 1994). The same displacement has also been implied in other areas where both species co-invade, attributed to avoidance behaviour during foraging (Pereira et al. 2016). Genomic investigation revealed close relatedness of New Zealand *V. germanica* haplotypes to populations in the U.K. and Western Europe (the most likely sources of the invasions) and Australia (Brenton-Rule et al. 2018).

The impacts and management of invasive *V. germanica* populations in New Zealand have been mostly studied in association with its congeneric co-invader *V. vulgaris*. Both species have been verified to present weak population genetic structures, indicating major bottleneck events upon introductions (Schmack et al. 2019). *Vespula* have a huge environmental impact in New Zealand due to predating native arthropods and outcompeting both invertebrates and vertebrates on sugary food sources in beech forest ecosystems (Harris 1991; Beggs and Wilson 1991; Lester and Beggs 2019). These wasps are able to reach world record population densities in such habitats, with up to 40 nests per hectare (Beggs et al. 1998). Colonies of both species can overwinter. In a beech forest system, 2–11% of colonies have been observed to overwinter, contributing with up to 64% of adults in a population (Plunkett et al. 1989). Also known as apicultural pests, with high population densities suggested to drive increased honeybee hive raiding frequencies when compared to their native environment in Eurasia (Clapperton et al. 1989a; Pusceddu et al. 2017). There is significant overlap between the two *Vespula* diet compositions in New Zealand when compared to other invading social wasps (Schmack et al. 2021); however, *V. germanica* may target native prey species at higher proportions and prefer large Hymenoptera and Orthoptera when compared to *V. vulgaris*, which may forage more often on Hemiptera and Lepidoptera (Harris 1991). First efforts to release *Vespula* natural enemies took place in the 1980s, with the introduction of the parasitoid wasp *Sphecophaga vesparum* (Donovan and Read 1987), which failed to significantly reduce population densities; the intro-

duction of different, more impactful agents was advised (Beggs et al. 2008). In 2021, two new species of biocontrol agents (predator hoverfly *Volucella inanis* and parasitoid beetle *Metoecus paradoxus*) were approved for import for release by the NZ Environmental Protection Authority (Environmental Protection Authority 2021; Stratford et al. 2024) but have not yet been widely released. *Vespula*-specific toxic bait traps have been developed in response to the New Zealand invasions and are widely applied in management efforts (Edwards et al. 2017).

Vespula vulgaris (Linnaeus, 1758)

Native range. Widespread in Eurasia (Archer 1989; Jacobson et al. 1978). Historically misidentified for *V. alascensis* as occurring in North America (Carpenter and Glare 2010).

Invasive range. French Polynesia: Society Islands (Tahiti) (Vallas, 2012; The International Barcode of Life Consortium, 2024); New Zealand: widespread (Clapperton et al. 1994). Also introduced elsewhere in Oceania: mainland Australia in 1958 (Johnston 1960), Tasmania in 1995 (Matthews et al. 2000); Europe: Iceland (Ólafsson, 1991); South America: Argentina and Chile (Masciocchi et al. 2010; Barrera Medina and Muñoz 2013).

Notes on invasion ecology. Possibly introduced to French Polynesia (Tahiti) in the 1990s; sampled through environmental DNA samples in 2007 (The International Barcode of Life Consortium 2024); fully established by 2012 at high altitudes (above 1000 m a.s.l.) (Vallas 2012). Altitude distribution possibly related to the species' thermal tolerance; overwintering colonies presumed possible due to mild climate. No formal studies on the invasion ecology of *V. vulgaris* have been carried out in French Polynesia. In New Zealand, early specimens were reported for the North Island, in Masterton, in 1923 (Thomson 1923), and later collected from two sites in Auckland in 1945 (Thomas 1960). Two males and a worker were found in April 1945 and an embryo nest with queen was found in November 1945 (Thomas 1960). The species is only considered to have established in the late 1970s (Lester and Beggs 2019); Bateman (1983) states that *V. vulgaris* queens were collected in Wellington from as early as 1978. In 1983, six nests were found in Dunedin during an investigation after a single worker was collected (Donovan 1984). Widespread across the country by the late 1980s and early 1990s, occupying higher altitudes (above 1000 m a.s.l., where co-invader *V. germanica* is absent; Clapperton et al. 1994). Genomic profiling shows six haplotypes of *V. vulgaris* in New Zealand, suggesting multiple introductions; populations are more closely related to those in Western Europe, the U.K., and Ireland (Lester et al. 2014).

For notes on the joint invasion ecology of *Vespula* in New Zealand, see "*V. germanica*" above.

Discussion

We have compiled a list of eleven alien social vespid species to have invaded the South Pacific, nine of which have evidence of establishment. The taxa represented in our inventory belong to four genera – *Polistes* (Polistinae), and *Dolichovespula*, *Vespa*, and *Vespula* (Vespinae) – and includes at least four distinct subspecies from two of the invasive species. Nine countries/territories showed records of established

invasive social Vespidae in the South Pacific, excluding Australia and Papua New Guinea. To the best of our knowledge, this inventory also contains the first formal report on the detection of the current incursion of *Vespa velutina* (an established and impactful invader in Europe) into New Zealand available in the scientific literature, alongside commentary on ongoing eradication efforts.

Exploring underlying trends regarding introduction dates, area of origin, and taxonomic diversity of invaders can provide valuable insights in understanding the invasive ecology of social wasps, and may help guide future biosecurity and conservation efforts. One barrier for a deeper understanding of the natural history and ecology of social Vespidae in the Pacific is the overall scarcity of data for the area. This is true not just for their invasion ecology and assessing their environmental impacts, but also for baseline biodiversity surveys. It is possible that our data is skewed by the small number of comprehensive historic records (French Polynesia: Cheesman 1928) or the heavier focus of published studies on specific subregions (New Zealand: Lester and Beggs 2019). It seems surprising that a relatively small number of taxa has successfully established across the Oceanic Islands, especially considering (1) the remarkable global spread of invasive social wasps and the ecological success achieved by a few of its species (Wilson Rankin 2021), and (2) the South Pacific's proximity to the social wasp biodiversity hotspot of Southeast Asia and western Australasia. While this may be a product of differing aspects of the natural history across social wasp species, we cannot rule out the possibility of underreporting, misidentification as similar already present species, and data deficiency in this understudied region. The advent of citizen science tools for biodiversity sampling such as iNaturalist can play a vital role in guiding future research efforts in data-deficient areas and help with early detection of new incursions (Campbell et al. 2023). Similarly, metabarcoding tools applied to environmental DNA samples may reveal unreported or cryptic invasions (Sezeng and van der Bank 2019; Young et al. 2021) and help guide survey and monitoring efforts for novel invaders (e.g. *Vespula vulgaris* in Tahiti: The International Barcode of Life Consortium 2024).

Another significant issue when seeking to unravel the history of social wasp incursions in the South Pacific is the lack of knowledge of the invasion pathways for established populations. Strong biosecurity practices have allowed for insights into how accidental introductions may happen – often associated with human goods in cargo ships in the trans-Pacific trade (Beggs et al. 2011). Still, a meagre minority of known introductions have available information on their *de facto* pathways, which are often speculative (such as the introduction of *V. germanica* in New Zealand through military aircraft in the 1940s: Thomas 1960). While robust evidence of probable introduction pathways can be difficult to obtain, even with current monitoring efforts (Courchamp et al. 2017; Hofman and Rick 2018), valuable insights on biological incursions may be gained through modern genomic tools. Phylogenomic methods can provide relatedness estimates between invasive populations and those across native ranges, often facilitated due to the prevalence of bottlenecks in the genetic structure of alien populations (Schmack et al. 2019; Tsuchida et al. 2014). Such studies have been done for *Polistes chinensis antennalis* (Tsuchida et al. 2014) and *Vespula vulgaris* (Lester et al. 2014) in New Zealand in the South Pacific, and elsewhere for other invaders (e.g. *Vespula germanica* in South Africa: van Asch et al. 2022). Knowledge on the probable origins of invaders, when associated with forensic data on trade and travel routes, can help fill the gaps in monitoring efforts and historical records (Cristescu 2016; Sherpa and Després 2021).

The fossil record of social Hymenoptera in the South Pacific constitutes yet another severe knowledge gap when considering the region's fauna and historic movements (Jourdan and Mille 2006). Some species that are present across islands (e.g. *Ropalidia impetuosa* in the Solomon Islands, Fiji, Australia and Papua New Guinea; Yamane and Kusigemati 1985) could not be unambiguously included in our inventory, although more than likely they spread from their original range into neighbouring islands. Whether these were a consequence of self or human-facilitated introductions may be impossible to ever determine. However, combining classic paleontological and paleogenetic methods can help deepen our understanding of the global movements of the social Vespidae before modern records were made (Knapp et al. 2021).

As evidenced in the above summaries, the Pacific Islands have been severely impacted by social wasp invasions. This is due to many factors, not least of which is human-facilitated opportunity for wasps to enter the islands. Incursion opportunities become more available alongside higher frequencies of human and freight travel between the wasps' native and introduced ranges. Increased connectivity due to globalisation is correlated with increased movement of social insects, especially in the early 20th century, as observed for the taxa listed here (Bertelsmeier 2021). The increase in incursion opportunities is also linked to the population of the wasp species in the source location, i.e. the more common the species, the more likely it is to be accidentally transported (Bertelsmeier 2021, Bertelsmeier and Keller 2018). Four of the most invasive Vespids in the Pacific are from such populations and these often reach very large densities in their introduced ranges. Bertelsmeier and Keller (2018) call these "invasive bridgehead populations" and assert that these facilitate further and faster spread to new areas (Bertelsmeier 2021). This is probably a key factor determining the successes of *Vespula germanica*, *V. vulgaris*, *P. dominula*, and very likely *P. olivaceus*, invading and establishing in new territories (Bertelsmeier 2021) when compared to less common sympatric species (for example *Vespula rufa* from the U.K.) (Fox-Wilson 1946). The existence of specific life history traits as a requirement (or at least a facilitator) of biological invasions may be one explanation for the lack of establishment from taxa such as *Ropalidia* in the Pacific, considering it is a speciose group inhabiting an adjacent geographic range.

Comparing the South Pacific social wasp fauna to other notable invaded ranges is challenging due to the unique ecological opportunity this region offers to alien species. When the wasps arrive at a new location in the Pacific, there is often an absence of native or otherwise present social wasps with which to compete for food, resources or nesting sites (Beggs et al 2011; Lester and Beggs 2019). Australia is possibly the most comparable area in terms of biogeography and invasion history. Similarly to other South Pacific nations, it is likely subject to migration patterns following island biogeography models (Nakamura et al. 2015), is geographically close to the social wasp biodiversity hotspot in Southeast Asia, contains a wide climatic range that locally overlaps with many Pacific territories (Chand et al. 2023), and has a history of impactful social vespid invasions over the last two centuries (*P. chinensis* to Sydney in 2008; *P. dominula* to Perth in 1977; *V. germanica* to Tasmania in 1959 and mainland in the 1970s-1990s; *V. vulgaris* to Victoria in 1958 and Tasmania in 1995; Carpenter and Brown 2022). However, Australia contains a diverse native community of social wasps (Carpenter and Brown 2022), and new invaders likely contend with significant niche competition during potential establishment. While human movements in the late 20th century likely facilitated the

spread of alien social wasps in Australia in a similar fashion to other South Pacific islands (and continue to do so), the two regions probably present significant ecological differences when it comes to establishment. It is not unlikely that Australia (and nearby islands with comparable native social vespid faunas) is a more invasion-resilient environment when compared to most other South Pacific islands, limiting invasions to the most competent invaders. This is somewhat supported by known failed establishments from past invasions (*P. olivaceus*, temporarily established in Brisbane in the mid-20th century; *Provespa nocturna* in Queensland in 1968; Carpenter and Brown 2022) Conversely, South Pacific invaders are likely limited by dispersal opportunities and Grinnellian niches, and their establishment could fit better under the enemy release hypothesis due to the lack of natural predators or competitors (Colautti et al. 2004). Australia's invasive social wasp fauna comprise four species and is less rich than the most invaded Pacific Nations (New Zealand, n=5; and French Polynesia, n=6), despite the country containing a much larger landmass which is closer to invader sources and has significantly higher current and historical overseas traffic rates than any other South Pacific nation (e.g. accounting for an average of 66.83% of all maritime port calls in Oceania between 2018 and 2023; United Nations Trade and Development statistics 2024). It also is worth noting that the four invasive social wasp species in Australia are well known invaders in other areas of the world (and the Pacific), further supporting the presumption that only highly capable invaders may be able to compete with the native fauna for establishment. Any comparisons, however, must be made carefully given the complex, multifactorial nature of biological invasions and the intrinsic biogeographic differences between Australia and the eastern South Pacific islands.

Globally, social wasps continue to invade new territories. There are eight species from three genera in the Vespidae that are leading the new invasions; three *Polistes* (Polistinae): *Polistes chinensis*, *P. dominula*, *P. versicolor*; three *Vespula* (Vespinae): *Vespula. germanica*, *V. pensylvanica*, *V. vulgaris*; and two *Vespa* (Vespinae): *Vespa mandarinia*, *Vespa velutina* (Wilson Rankin 2021, Lester and Beggs 2019). So far, *Vespa* have not successfully established in the Southern Pacific Islands, but the *Vespa tropica* establishment in Guam (Rosario et al. 2016) constitutes a warning for biosecurity efforts. Furthermore, as global climatic patterns continue to shift in response to human action, it is more than likely that the movements of alien species may be affected (Bertelsmeier 2021, Menzel and Feldmeyer 2021). The shifting climate may increase the suitability for some species of invasive social wasps to thrive in some areas, while some areas with historically ideal conditions may become unsuitable (Lester and Beggs 2019). For instance, as areas increase in temperature and become drier there may be an increase in perennial *Vespula* nests, but *Vespula* colonies may struggle in areas that see increased rainfall due to climate change (Lester and Beggs 2019). This may result in the expansion of the invasive ranges for already introduced species and the arrival of novel invaders with the opening of new ecological niches concerning the thermal tolerance and physiological thresholds of social wasps (Menzel and Feldmeyer 2021).

Several management methods are being developed to control invasive *Vespula* and *Polistes* species, such as direct insecticide application to nests, toxic baiting, classical biological control, lure-and-kill, as well as molecular based techniques like RNA interference and gene drives (Lester and Beggs 2019). Currently, the most effective method available for local management of *Vespula* is using fipronil-infused baits (Lester and Beggs 2019), particularly in areas in which the wasp populations

are protein limited. Recent work on classical biological control of *Vespula* in New Zealand and Australia aims to build off earlier work on the parasitoid, *Sphecophaga vesparum* to lower wasp populations (Donovan and Read 1987; Hester et al. 2024). Two other biological control agents are also being pursued alongside *Sphecophaga vesparum* in New Zealand, the predatory hoverfly *Volucella inanis*, and the parasitoid beetle *Metoecus paradoxus* (Stratford et al. 2024). Feasibility for using classical biological control for three invasive *Polistes* species in New Zealand is also being considered (Brown 2021). Due to the lack of native social insects in many of the Pacific Islands, classical biological control may also be a promising management tool that should be investigated. The best control method of invasive social wasps remains to be prevention of their establishment by instituting strong biosecurity efforts at the borders. Ideally, each island accepting trade goods and tourists would have the ability to detect any new incursion and have the authority and resources to respond rapidly in order to eradicate the incursion before they can spread.

Conclusion

Mapping the alien fauna of the South Pacific Oceanic Islands is not a straightforward task. The overall lack of baseline knowledge for the region, combined with a patchy understanding of invasion, and self-introduction histories and pathways, creates challenges for understanding social vespid invasion ecology. Organizing the existing knowledge geographically and chronologically allows us to start visualizing how human movements have historically shaped the wasp invasions for that area in the last three centuries. This database presents a starting point for future, in-depth, and hopefully broad investigations on the invasive biology of wasps in the Pacific, while also serving as a resource for conservation, management, and biosecurity efforts.

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The authors have declared that no competing interests exist.

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Use of AI

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Author contributions

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Data availability

The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, and are available at https://ipt.pensoft.net/resource?r=alien_social_wasps_pacific&v=1.0.

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Supplementary material 1

Earliest known records of invasive social wasps (Hymenoptera: Vespidae: Polistinae & Vespinae) in the South Pacific, excluding Australia and Papua New Guinea

Authors: Mateus Detoni, Lynley Hayes, Robert L. Brown

Data type: csv

Explanation note: This dataset compiles the distribution of alien social wasp species found in the Oceanic Islands of South Pacific, excluding Australia and Papua New Guinea. Each entry provides information on a species' earliest record of invasion in one nation or territory of South Pacific. Taxa are organised alphabetically by subfamily, genus, species, and subspecies (if known). Data on native range, current introduced ranges outside of the South Pacific and/or in Australia and Papua New Guinea, area of record, establishment status, evidence analysed, and bibliographic reference are included for each entry.

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Link: https://doi.org/10.3897/neobiota.106.160421.suppl1

Supplementary material 2

References for individual taxa global distribution data for the invasive social wasps of the South Pacific

Authors: Mateus Detoni, Lynley Hayes, Robert L. Brown

Data type: pdf

Explanation note: This file lists the bibliographic references sourced from the Global Biodiversity Information Facility (GBIF) used to construct the maps in Figs 2, 3 showing global distribution and invasive ranges of the alien species listed in the main text..

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